Pedobiologia 35, 285–296 (1991)
Gustav Fischer Verlag Jena

University of Jyväskylä, Department of Biology, Jyväskylä, Finland

Mineralization of C, N and P in relation to decomposer community structure in coniferous forest soil

H. SETÄLÄ, M. TYYNISMAA, E. MARTIKAINEN and V. HUHTA

With 3 figures

(Accepted: 91-01-31)

1. Introduction

There is a general agreement that the presence of fauna exerts positive influence on the soil processes, such as decomposition and nutrient leaching (see reviews by R. V. ANDERSON *et al.*, 1981a; J. M. ANDERSON & INESON, 1983; SEASTEDT, 1984; INGHAM *et al.*, 1985). The authors have recently been studying these mechanisms in long-term experiments with coniferous forest soil, using a laboratory design simulating the complexity of the natural environment (HUHTA & SETÄLÄ, 1990; SETÄLÄ & HUHTA, 1990; SETÄLÄ *et al.*, 1990). From these studies it is evident that the influence of the fauna on the parameters measured is not independent of the community structure (combinations of taxa, including competitive and predator-prey-relationships). The experiments reported here were planned to test some hypotheses which arose while monitoring the main experimental programme. The aim was to compare some simple combinations of animal taxa, with communities of one taxon or trophic group, with more complex communities associated with the main experiments.

2. Material and methods

Seven different combinations of sterilization-reinoculation treatments were included in the experiment:

- Control with microbes (it was assumed that Protozoa which passed through a 10 µm filter were present in all treatments).
- Addition of microbivorous nematodes (N).
- Predatory nematodes (P) added with (N).
- Enchytraeids (E) added, without nematodes.
- Enchytraeids (E) added with (N).
- Collembolans (C) added, without nematodes.
- Collembolans (C) added with (N).

In the text these treatments are grouped into three sets with the respective symbols "Control, N, P + N"; "Control, E, E + N"; and "Control, C, C + N".

The material used for the experiment was raw humus soil (organic layer only, initial *p*H 4.0, loss on ignition 76%, C = 41.7% of dry mass, N = 1.10% of dry mass), taken on 30 May 1988 from a *Myrtillus*-type spruce stand near Jyväskylä, Central Finland. This was sieved through a 5 mm mesh sieve and thoroughly mixed. To increase the complexity of the substrate, crushed birch litter (*Betula pendula*) was added. The litter (whole leaves, overwintered under snow and collected on 20 May) was dried, and after removing the pedicules, the leaves were firstly rinsed in tap water, and then in distilled water. After that the material was oven-dried at 80 °C for 24 h and crushed by hand.

The size distribution (in % of total mass) of the resulting fragments < 1 mm/1 – 2 mm/> 2 mm was 29/53/18. Aliquots of 30 g moist humus ($\triangleq$ 9.1 g dry mass) were weighed and mixed with 0.5 g (dry mass) litter, and lightly packed into 174 ml glass jars. Fifteen replications were prepared for each

treatment; a total of 105 jars. The jars containing the experimental materials were then placed in a commercial microwave oven for 3 minutes (2450 MHz, 620 W measured output). This treatment eliminates fauna (see below) while leaving a residual inoculum of fungi and bacteria. After treatment the jars were sealed with metal lids. The lids contained holes (10 mm diam.) that were kept sealed with sterilized cotton plugs during the experiment.

Soil microbiota was re-inoculated into all replicates from a suspension of 20 g soil (fresh) mixed for 30 sec using a vibromixer in 500 ml of tap water. After 2 h, 30 ml of this mix was taken, allowed to settle for 1 h, and filtered twice through a 10 µm filter. Distilled water, 120 ml, was added to the filtrate and mixed, and 1 ml of suspension was sprayed onto each sample. This was done on 3 June ("Day 0"), after which time the jars were incubated in a controlled temperature cabinet at +16 °C.

Nematodes were extracted from the same soil with the wet funnel method (SOHLENIUS, 1979). Contents of collecting tubes from several funnels were inspected under a dissecting microscope and small microbivorous nematodes were removed and placed with a pipette into tap water. 1.5 ml of the water + nematodes suspension (during continuous mixing) was added to each replicate of the treatments N, P + N, E + N and C + N. Test samples revealed that 1.5 ml of suspension contained an average of 32 bacterial feeding nematodes belonging to the taxa *Plectus*, Acrobeliinae and (occasionally) *Rhabditis*. The rest of the replicates received 1.5 ml of micro-waved tap water each. The nematode inoculation took place on Day 4.

Predatory nematodes *(Mononchus spp.)* were extracted from a stored soil sample containing unusually high numbers of *Mononchus*. Fifteen specimens (the lengths ranging between 500 – 1000 µm) in 2 ml of water, were added to each P + N replicate on Day 18, and 22 additional specimens on Day 27. Simultaneously, all other replicates received the same amount of micro-waved tap water.

Enchytraeids (*Cognettia sphagnetorum* VEJD.) were extracted with the wet funnel method (O'CONNOR, 1962) from intact cores taken from the same soil. After extraction they were removed with a hooked needle, placed in cold tap water, and stored overnight at 5 °C. The following day they were moved individually into the treatments E and E + N. Each replicate received 20 specimens on Day 6, 12 more on Day 11, and 30 on Day 27; thus the total inoculum was 62 worms per sample.

Each replicate for the treatments C and C + N received 30 specimens of *Onychiurus armatus* (TULLB.), reared at 15 °C in Petri dishes on Plaster of Paris, and fed with commercial yeast. The culture was obtained from the Department of Animal Ecology, University of Lund, Sweden.

The evolution of CO_2 from five random replicates from each treatment was measured weekly (twice a week until Day 20) with an URAS 7N carbon analyser. At the start of measurement, the cotton plug in the lid of the jar was replaced with a rubber septum, through which a 5 ml air-sample was taken with a syringe. Another sample was taken after a further incubation period of 1 h. The analyzer was connected to a microcomputer programmed to calculate the CO_2 increment and express the result in mg CO_2 per g dry mass of the sample.

The cultures were sampled destructively to determine animal populations, *p*H, and water-soluble NH_4^+ and PO_4^{3-} after incubation for approximately 1, 2 and 4.5 month (Days 25, 60 and 137). On each occasion, 5 replicates of each treatment were removed. For the nutrient analyses, 30% (fresh mass) of the contents of each jar was mixed with 100 ml distilled deionized water. After settling for 2 – 3 h the suspension was filtered (glass fiber filter, Macherey-Nagel & Co.), and the concentrations of NH_4^+ and PO_4^{3-} in the filtrate were measured photometrically using standard methods (SFS 3032 for NH_4^+, and INSTA-VH 22 for PO_4^{3-}). The results were calculated as amounts of N and P per g dry matter. The *p*H values of the filtrates were also measured.

We measured water extractable NH_4^+ and PO_4^{3-} instead of exchangeable nutrients so that the results were comparable to the main experiments where measurements were made of nutrients dissolved in simulated rainfall (SETÄLÄ *et al.*, 1990).

Nematodes were extracted from 20% subsamples using the wet funnel method (SOHLENIUS, 1979). The animals were counted under a dissecting microscope at 50× magnification. For the estimation of biomass, ca. 50 random specimens extracted on Day 137 were measured, and their masses determined according to ANDRASSY (1956). The average dry mass of individual so obtained, 0.025 µg, was used in the calculations.

In the treatments E and E + N, 50% of the substrate was used for the extraction of enchytraeids using the method of O'CONNOR (1962). The animals were counted separately in size classes with intervals of 2 mm, after which their biomass could be estimated according to ABRAHAMSEN (1973).

In the treatments C and C + N, *D. armatus* was extracted with a flotation method: one half of each sample was gently mixed with 200 ml of water, after which the animals could be picked from the surface. They were counted in size classes with 0,8 mm intervals and their biomass was estimated using the formula of PETERSEN (1975) for laboratory populations.

The faunal respiration was estimated according to PERSSON *et al.* (1980), interpolated to the incubation temperature. (See also discussions by KLEKOWSKI *et al.* (1972) for nematodes, and PERSSON & LOHM (1977) for enchytraeids and microarthropods.)

Paired t-tests were used for treatment comparisons, with the exception of CO_2 evolution, which was tested using ANOVA with repeated measurements. In addition to this experiment we repeated the set "control, N and P + N" in the same way as described above, with the following exceptions:

The soil for the experiment was taken from another site and contained more mineral matter (loss on ignition 32.6%). The microcosms were smaller, containing 15.0 g (fresh; 7.6 g dry) humus and 0.25 g (dry) crushed birch litter. The microbial inoculum was filtered through 5 µm instead of 10 µm filters. "Day 0" was 6 September, 1988. On Days 2 and 3 each microcosm was sprayed with 2 ml of "condensed" nematode suspension (controls with micro-waved tap water), containing an average 740 nematodes, mainly bacterial feeders but also including some fungal feeders, such as *Aphelenchoides*. Treatment P + N received 60 preadatory *Mononchus* specimens per microcosm. Deionized water was later added to each replicate: 3 ml on 25 Nov., 4 ml on 24 Dec., and 8 ml on 27 Jan. The CO_2 measurements were carried out weekly, while the contents of the jars were analysed at the termination of the experiment (Day 153, 7 Feb. 1989).

The purpose of this experiment was to check and confirm the results of the set "Control, N, P + N" by introducing dense populations from the very beginning. To distinguish this experiment from the main one, the symbol "P + N II" will be used.

3. Results

3.1. Animal populations and biomasses

The elimination of soil fauna by microwaving proved to be very effective. In the two experiments, no contamination was observed in any treatment not re-inoculated with animals. (It should be noted that the Control treatments included an inoculum of protozoans that passed the filter).

In all the treatments with nematodes, the nematode populations were still very low on Day 25, though several-fold higher than the introduced populations (table 1). By Day 60 they had reproduced dramatically, up to 2600 times the original numbers. By the end of the experiment, only the treatment E + N showed some further increase, while a decreasing trend was observable in the other treatments.

Table 1. Numbers of nematodes, enchytraeids (*C. sphagnetorum*) and collembolas (*O. armatus*) (mean ± S.D.; n = 5) per g (d.m.) of substrate.

	Day 25	Day 60	Day 137
Nematoda			
N	23.8 ± 13.3	8708 ± 1426	7670 ± 1908
P + N	17.6 ± 16.3	6216 ± 240**	1778 ± 1032***
E + N	15.3 ± 10.6	9186 ± 4964	11701 ± 1136**
C + N	19.9 ± 10.9	6519 ± 2240	4647 ± 1373*
C. sphagnetorum			
E	4.1 ± 0.7	17.1 ± 2.5	107.2 ± 17.8
E + N	3.8 ± 0.4	14.0 ± 4.0	72.0 ± 29.9
O. armatus			
C	2.7 ± 1.1	12.4 ± 4.8	42.6 ± 13.8
C + N	2.8 ± 0.9	11.8 ± 4.6	49.7 ± 11.1

Note: Treatment symbols: N = microbivorous nematodes, P = predatory nematodes, E = Enchytraeidae, C = Collembola. Asterisks indicate significant differences from N.

In the presence of predatory nematodes the total abundance had sharply decreased, while the presence of the enchytraeids had an opposite effect. It should be noted that the data for nematodes in table 1 refer to the total nematode populations though predatory species were scarce in the samples checked.

In Expt. P + N II, the predatory nematodes reduced the populations of bacterial feeders to a fraction when compared with the community without predators, and the populations of *Mononchus* also reached a considerable density: On Day 153 there were 3919 ± 1171 nematodes (no predators) in N, and 77 ± 105 bacterial feeders + 28 ± 14 *Mononchus* in P + N, as calculated per g d.m.

The biomasses of nematodes were not estimated in the first experiment. At the end of Expt. P + N II the total nematode biomass was 48.5 μg g^{-1} d.m. in N, and 16.8 in P + N; the bulk in the latter was composed of *Mononchus* (97%). Thus, by the end of the experiment these predators had consumed most of their food. The feeding had been selective: *Rhabditis* had almost disappeared in the presence of *Mononchus*.

The reproduction of enchytraeids and collembolans was more gradual; their populations continued to increase 3 to 6-fold between Days 60 and 137 (table 1). The presence of nematodes may have depressed the enchytraeid population (Day 137), while no influence on *O. armatus* was detected (tables 1 and 2).

Table 2. Biomasses (μg d.m.) of Enchytraeidae and Collembola (mean ± S.D.) per g (d.m.) of substrate.

	Day 25	Day 60	Day 137
C. sphagnetorum			
E	97.5 ± 21.1	197.4 ± 59.7	1278.0 ± 399.9
E + N	91.8 ± 32.8	200.6 ± 76.5	723.7 ± 276.2
O. armatus			
C	45.3 ± 18.0	99.8 ± 30.9	363.3 ± 144.7
C + N	47.4 ± 9.1	119.7 ± 50.0	345.3 ± 71.1

Note: To obtain rough estimates for nematodes, multiply numbers in table 1 by 0.025. Treatment symbols: see table 1.

The biomasses of Enchytraeidae and Collembola increased roughly in proportion to their numbers (table 2). However, there were changes in the average size of individuals. The size categories above 7 mm were virtually absent in the final set of enchytraeid samples, while in *O. armatus* plenty of small specimens (below 1 mm) were present on Days 60 and 137, indicating continuous reproduction.

3.2. Respiration

The flush of CO_2 at the beginning of the experiment is typical of microbial respiration in soil materials following partial sterilization (ALEXANDER, 1977). The peak was reached on Day 7 (70 – 75 μg CO_2 g^{-1} d.m. h^{-1}) after which the respiration rapidly declined to ca. 35 μg g^{-1} h^{-1} by Day 17. In the early phases the treatments did not differ significantly from each other, except on Day 13, when the samples inoculated with Collembola or Enchytraeidae showed increased respiration (C and N + E > N and Control).

After Day 20 the respiration gradually decreased. In combination with the growth and establishment of the animal populations, further differences between the treatments could be detected. Without exception, cumulative respiration was higher in the soil re-inoculated with fauna, than in soil with microbes alone (fig. 1). Bacterial feeding nematodes alone had a slight effect, but the presence of predators doubled the "additional" CO_2 production. The trend was very similar in Expt. P + N II, although the average respiration per unit dry

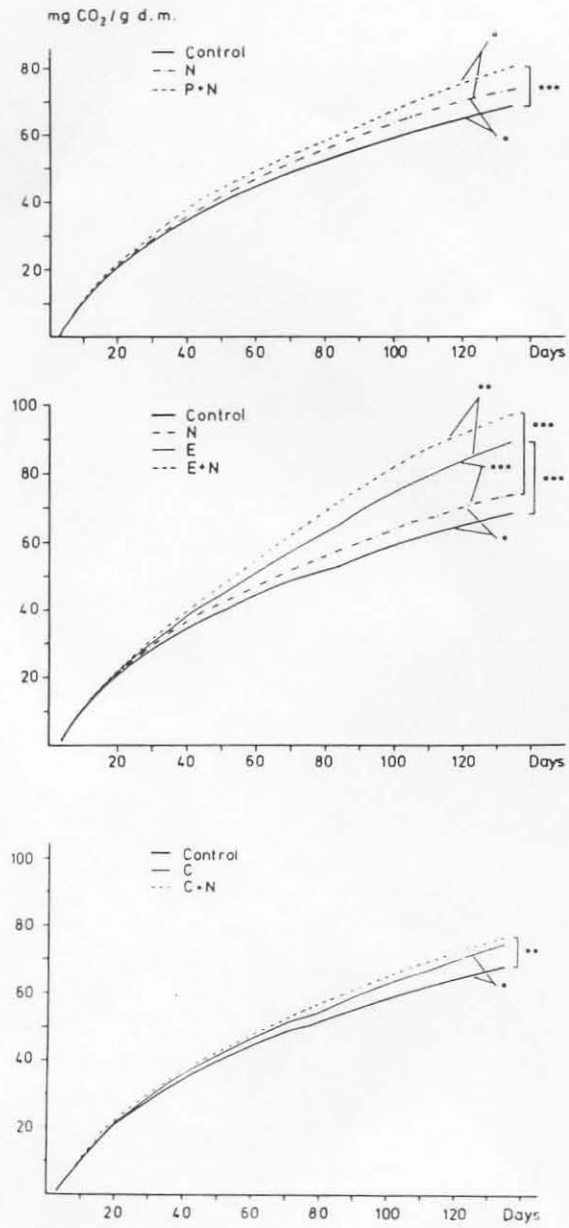

Fig. 1. Cumulative evolution of CO_2 in the three sets of treatments. Symbols: N = microbivorous nematodes, P = predatory nematodes, E = Enchytraeidae, C = Collembola. Asterisks indicate significant differences over the whole experiment: (* = $p < 0.05$, ** $p < 0.01$, *** = $p < 0.001$; ANOVA for repeated measurements).

matter was much lower due to the high content of mineral material. The cumulative respiration by the end of the experiment P + N II was 51.48 mg CO_2 g^{-1} d.m. in Control, 53.58 mg in N, and 57.39 mg in P + N.

O. armatus either alone or together with nematodes had approximately the same effect as did nematodes alone. The enchytraeid *C. sphagnetorum* alone caused an increase in

respiration, which was even greater when together with nematodes (cumulative CO_2 production by Day 137 43% more than in Control, and 33% more than in N).

The estimated respiration of the fauna was negligible during the first weeks, but together with the growth of animal populations and decrease in total activity the faunal contribution reached a considerable proportion (table 3). It was lowest in the treatment P + N, and highest in the treatments with enchytraeids, where the faunal biomass also was highest (table 2).

3.3. Release of nitrogen and phosphorus

The amount of water-extractable NH_4^+ increased considerably during the experiment, while that of PO_4^{3-} showed only a slight increase (figs. 2 & 3). The faunal inoculations showed significant effects on the water-soluble nutrient contents even at the first destructive sampling, when the populations were still low compared to later in the experiment.

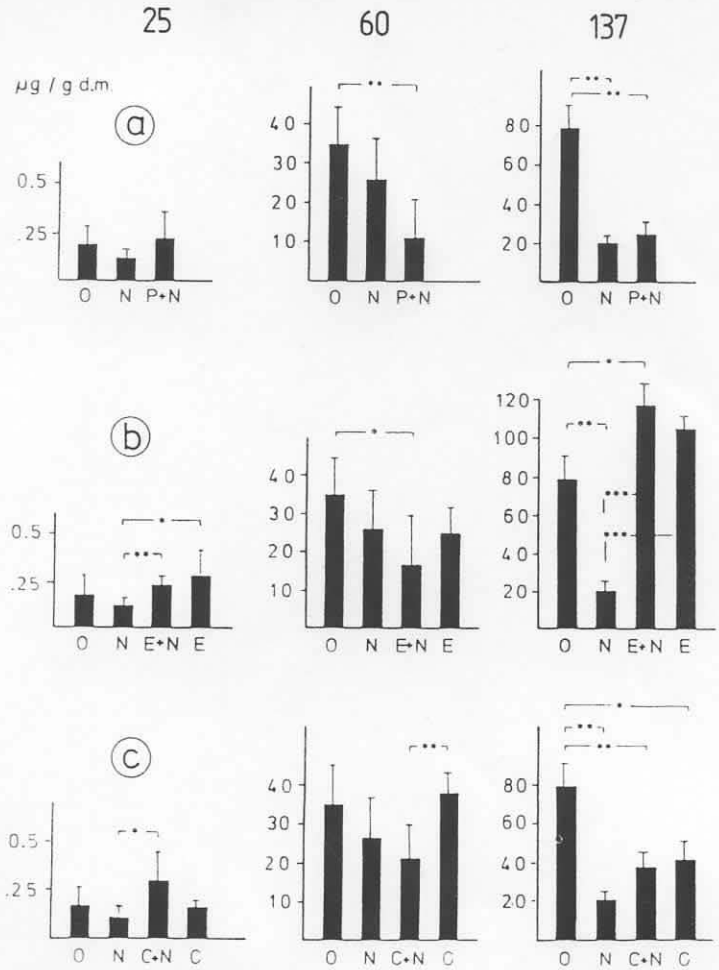

Fig. 2. Water-extractable NH_4^+-N (µg N g^{-1} d.m., mean ± S.D.) in the three sets of treatments (a, b, c) on Days 25, 60 and 137. For treatment and other symbols, see fig. 1. (0 = control.) The asterisks denote significant differences between treatments (Student's t-test). Note differences in scales between dates.

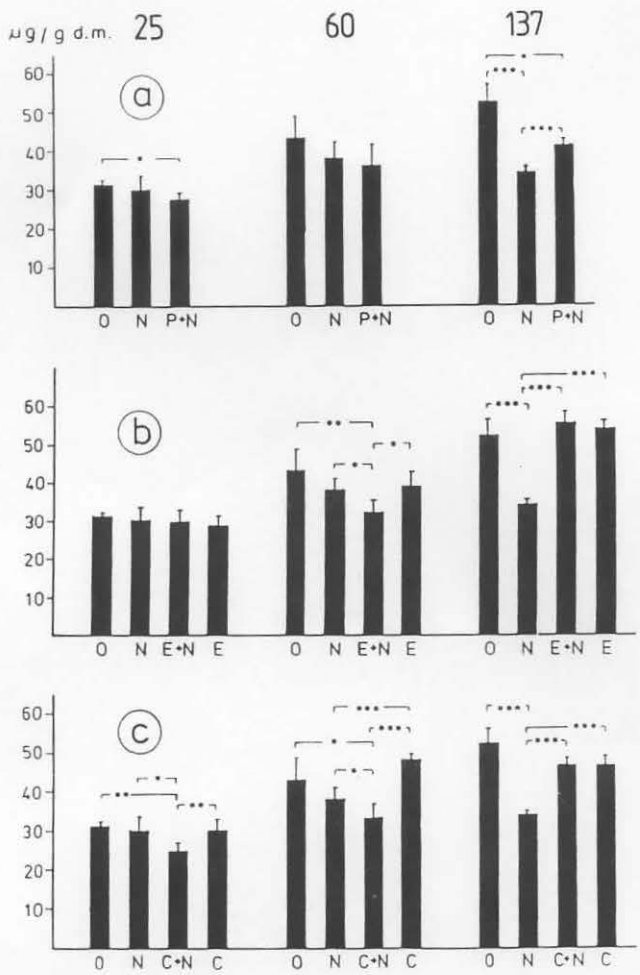

Fig. 3. Water-extractable PO_4^{3-}-P (µg P g^{-1} d.m., mean ± S.D.). For explanations see fig. 2.

Table 3. Momentary total (measured) and faunal (estimated) respiration (µg CO_2 g^{-1} d.m. h^{-1}) at the end of experiment.

	Total	Nematoda	Enchytraeidae or Collembola	Faunal, % of total
Control	**10.40**	–	–	–
N	**9.87**	2.65	–	27
P + N	**14.14**	0.61	–	4
E	**12.54**	–	6.41	51
E + N	**14.32**	4.04	4.31	58
C	**15.89**	–	1.87	12
C + N	**11.99**	1.60	1.87	29

Note: Treatment symbols: see table 1 or fig. 1.

Nematodes (with or without predators) decreased the availability of nitrogen substantially by the last sampling date (Day 137), whilst there was no difference between treatments N and P + N. The same holds for phosphorus, but the difference was smaller. The treatment P + N released more PO_4^{3-} than did microbial feeders alone. On Day 60, P + N released less NH_4^+ than did the control.

In Expt. P + N II the differences in the release of NH_4-N and PO_4-P were slight, but somewhat more phosphorus was leached from P + N (152 μg g^{-1} d.m.) than from N (141 μg) and Control (135 μg; $P < 0.01$). The amount of NH_4^+ remained below the detection limit in many replicates. NO_3^- was also analysed; the community with predators released significantly more (0.68 ± 0.29 μg NO_3^--N g^{-1} d.m.; hardly measurable amounts in N and Control). Since the drying of the substrate surface (Expt. P + N II), extra water was added in the microcosms 1 – 2 weeks before the nutrient analyses. This caused a flush in microbial activity, which may have resulted in increased immobilization of nutrients. None the less, the predatory nematodes resulted in a net mobilization of inorganic N and P.

Enchytraeids, both alone and with nematodes, increased the leaching of NH_4^+ considerably in comparison with nematodes alone (fig. 2). This was observable already on Day 25, while on Day 60 there was no difference. The influence of enchytraeids on the leaching of PO_4-P was similar but smaller (fig. 3, Day 137). There were few differences in comparison with control.

O. armatus had a very similar effect on the soluble N and P as had *C. sphagnetorum* (figs. 2 & 3). However, the collembolan together with nematodes in several cases released less nutrients than did *O. armatus* alone (Day 25 PO_4^{3-}, Day 60 NH_4^+ and PO_4^{3-}). In these cases the leaching was significantly less than from the control with microbes only.

3.4. *p*H

There were several small but significant differences in the leachate *p*H between the treatments. On Day 60, the *p*H was lower in the treatments P + N, E, and C, than in the control, while the opposite was true in E and E + N on Day 137 ($P < 0.01$). The control *p*H increased from the initial 4.0 to 5.0 during the experiment, and the differences between treatments remained below 0.35 units. In Expt. P + N II the differences were insignificant.

4. Discussion

The animal populations in our experiments reached extremely high densities in comparison with natural populations in similar soils (HUHTA *et al.*, 1986). Calculated per unit area, there were over ten times more nematodes, roughly tenfold numbers of *C. sphagnetorum* and twice as many *O. armatus* alone than all Collembola in the field. The biomasses were roughly tenfold, threefold and tenfold, respectively. This is not unexpected in laboratory conditions, where the soil moisture is kept appropriate for hydrophilous fauna and the natural range of competitors/predators is absent. In our first experiment the evaporation was very slow, and despite that no additional water was given during the 4.5 months, the soil lost only 33% of its initial water (the water content was still ca. 59% at the end). (In Expt. P + N II the evaporation was higher, and the microcosms were watered at times.) For example ABRAHAMSEN (1971) and SOHLENIUS (1985) obtained high population densities of enchytraeids and nematodes, respectively, in the absence of other taxa in their laboratory cultures.

In most studies made in the laboratory, single species communities have been used without potential predators or competitors. In our experiment the emphasis was put on different combinations of the soil fauna, two taxa at a time. In two cases only did the two taxa present together exert influence on each other. Predatory nematodes appeared to greatly reduce the populations of microbial feeders, which was particularly apparent in

Expt. P + N II. The depression of microbial-feeding nematodes by predatory mites has been shown in a field study by SANTOS & WHITFORD (1981) and in the laboratory by MARTIKAINEN & HUHTA (1990). Predation, in general, suppressed the microbivorous fauna in the experiments of HUHTA & SETÄLÄ (1990). The increase of nematodes in the presence of *C. sphagnetorum* was unexpected, and could be of short duration (the populations could not be checked between Days 60 and 137, neither after Day 137).

The estimated respiration by the fauna at the end of our experiment was extremely high when compared with corresponding calculations from field studies (HUHTA & KOSKENNIEMI, 1975; PERSSON *et al.*, 1980; PETERSEN & LUXTON, 1982). Various uncertainties involved in the estimation of faunal respiration may lead to considerable over- (and under-) estimations, but it must also be considered that the animal numbers and biomasses were very high in our experiments in relation to field abundances.

The positive influence of the fauna on the total soil respiration in our experiments was generally consistent with several other studies (e.g. HANLON & ANDERSON, 1979; HANLON 1981a; R. V. ANDERSON *et al.*, 1981b; BENGTSSON *et al.*, 1988; SETÄLÄ *et al.*, 1988). The results give strong support to our hypothesis that a complex faunal community has a synergistic effect on carbon mineralisation. The lowest respiration was measured in the control, followed by bacterial-feeding nematodes, or collembolans together with microbes. Enchytraeids alone with microbes resulted in a more elevated activity than did the other two taxa. With all combinations tested, more CO_2 evolved from the systems with two animal taxa present. The presence of predatory nematodes increased the activity in spite of essentially lower total biomass of nematodes. Thus, our interpretation is that predation stimulated the activity of the decomposer community in a way which is not simply additive, but interactive with other biotic components. The most effective taxon was the enchytraeid *C. sphagnetorum* which alone had more influence than any taxa in combination, and together with nematodes they further increased the total respiration.

STANDEN (1978) showed that the respiration in the faeces of *C. sphagnetorum* was higher than it was in their food material. PONGE (1985) also regarded the excreta of enchytraeids as good substrate for bacterial growth. Thus the higher respiration in the presence of enchytraeids could be a consequence of enhanced microbial activity in their fresh faeces. On the other hand, the stimulation of decomposition by the soil fauna may also include changes in the physical characters of the substrate. HANLON (1981b) demonstrated a non linear relationship between respiration and particle size, which resulted in inhibitory effects of litter break down to very small particles. In our experiment there was clearly more material with fine particle-size in the presence of enchytraeids (observable under a dissecting microscope, or even by eye). Thus at the middle of the experiment, the enhanced decomposition rate under the influence of enchytraeids may be explained by the microbial activity of their casts, while the respiration of the enchytraeids contributed more at the end. The latter situation would probably not have continued if the experiment had lasted longer.

It is generally considered that the soil fauna enhances the release of nutrients from decomposing litter (R. V. ANDERSON *et al.*, 1981a; BÅÅTH *et al.*, 1981; INESON *et al.*, 1982; J. M. ANDERSON *et al.*, 1983; HUHTA *et al.*, 1988). In the present experiment this was true in two cases only (E + N and P + N II). In all other cases when significant effects were recorded, the fauna rather seemed to cause an immobilization of nutrients. However, when the comparison is made between enchytraeids or collembolans vs. nematodes alone, their influence was positive, i.e. resulting in an increase of leachable nutrients. Two taxa together either increased or decreased the leaching in comparison with either taxon alone.

The elimination of microbial feeders (especially nematodes) was more complete in this experiment than it was in our "main study" (HUHTA & SETÄLÄ, 1990; SETÄLÄ & HUHTA, 1990; SETÄLÄ *et al.* 1990). Nevertheless, the Control in the present study included two links of food chain: Bacteria (+Fungi) and Protozoa, which were only partially eliminated. Protozoa are known to be more efficient bacterial consumers than are nematodes (CLARHOLM, 1982; BRYANT *et al.*, 1982; WOODS *et al.*, 1982), and WOODS *et al.* (1982)

showed that the composition of microbial-feeding community affects the net mineralisation of nutrients.

The idea generally accepted by soil biologists is that during the decomposition of nutrient-poor substrates microbes tend to immobilize available nutrients into their biomass, and hence result in a slow-down of decomposition, its rate depending on the turnover of the microbial biomass. This turnover is assumed to be greatly accelerated by predation by Protozoa and Nematoda (R. V. ANDERSON *et al.*, 1981a, b, WOODS *et al.*, 1982). Our results indicate that in the absence of the next link in the food chain (predatory nematodes), there may be another step of nutrient immobilization in the biomass of microbial feeders, unless the nutrients are further circulated through higher levels of the food-chain. It is, however, obvious that the effect of predators in the field is not as distinct as it was in our laboratory experiment of rather short duration. The accumulation of nutrients in the faunal biomass cannot continue after a biomass limited by the environment has been reached. Predatory nematodes occur very sparsely in coniferous forest soils, while nematode-feeding mites are abundant (HUHTA *et al.*, 1986). Predation may result in considerable reduction of nematode populations (SANTOS & WHITFORD, 1981; ELKINS & WHITFORD, 1982; MARTIKAINEN & HUHTA, 1990).

The enchytraeid *C. sphagnetorum* was observed to have the strongest influence on both respiration and nutrient leaching. This is a typical and abundant inhabitant of coniferous forest soil (PERSSON *et al.*, 1980; HUHTA *et al.*, 1986). Due to the low representation of other fauna typical to coniferous soils, e.g. Oribatida, the relative role of enchytraeids may have been overestimated in the present study. The higher biomass of *Cognettia* should also be emphasized. J. M. ANDERSON *et al.* (1983) reported that Collembola released more NH_4^+ from deciduous litter than did enchytraeids, when the figures were related to the animal biomass. *O. armatus* occurs only sporadically in spruce forests in Finland, while other related species like *O. absoloni* and *Mesaphorura yosii* are abundant (HUHTA *et al.*, 1986).

5. Acknowledgements

The study was granted by the Council of Sciences, Academy of Finland. We wish to express our cordial thanks to M. BOUCELHAM and J. SALMINEN for carrying out a major part of the routine work, and M. KAUPPINEN for his help with statistical analysis. Dr. phil. INESON, Institute of Terrestrial Ecology, U.K., Dr. JONATHAN ANDERSON, University of Exeter, U.K. and Dr. DAVID H. WRIGHT, University of Georgia, U.S.A., kindly read the manuscript and provided valuable comments.

6. References

ABRAHAMSEN, G., 1971. The influence of temperature and soil moisture on the population density of *Cognettia sphagnetorum* (Oligochaeta: Enchytraeidae) in cultures with homogenized raw humus. Pedobiologia **11**, 417–424.

– 1973. Studies on body-volume, body-surface area, density and live weight of Enchytraeidae (Oligochaeta). Pedobiologia **13**, 6–15.

ALEXANDER, M., 1977. Introduction to soil microbiology. 2nd ed. Wiley & Sons, New York, pp. 467.

ANDERSON, J. M., & P. INESON, 1983. Interactions between soil arthropods and micro-organisms in carbon, nitrogen and mineral element fluxes from decomposing leaf litter. *In:* J. A. LEE, S. MCNEILL & I. H. RORISON (eds.), Nitrogen as an ecological factor. Blackwell Scientific Publications, Oxford, pp. 413–432.

– R. V., D. C. COLEMAN & C. V. COLE, 1981a. Effects of saprotrophic grazing on net mineralization. *In:* F. E. CLARK & E. ROSSWALL (eds.), Terrestrial nitrogen cycles. Ecological Bulletins **33**, 201–215.

– D. C. COLEMAN, C. V. COLE & E. T. ELLIOTT, 1981b. Effect of the nematodes *Acrobeloides sp.* and *Mesodiplogaster lheritieri* on substrate utilization and nitrogen and phosphorus mineralization in soil. Ecology **62**, 549–555.

– J. M., P. Ineson & S. A. Huish, 1983. The effect of animal feeding activities on element release from deciduous forest litter and soil organic matter. *In:* P. H. Lebrun *et al.*, (eds.), New trends in soil biology. Dieu-Brichart, Ottignies-Louvain-la-Neuve, pp. 87–100.
Andrassy, I., 1956. Die Rauminhalts- und Gewichtsbestimmung der Fadenwürmer (Nematoden). Acta Zool. Acad. Sci. Hung. **11**, 1–15.
Bååth, E., U. Lohm, B. Lundgren, T. Rosswall, B. Söderström & B. Sohlenius, 1981. Impact of microbial-feeding animals on total soil activity and nitrogen dynamics – a microcosm experiment. Oikos **37**, 257–264.
Bengtsson, G., M. Berden & S. Rundgren, 1988. Influence of soil animals and metals on decomposition processes: a microcosm experiment. J. Environ. Quality **17**, 113–119.
Bryant, R. J., L. E. Woods, D. C. Coleman, B. C. Fairbanks, J. F. McClellan & C. V. Cole, 1982. Interactions of bacterial and amoebal populations in soil microcosms with fluctuating moisture content. Appl. Environ. Microbiol. **43**, 747–752.
Clarholm, M., 1982. Protozoan grazing of bacteria in soil. Microbial ecology **7**, 343–350.
Elkins, N. Z., & W. G. Whitford, 1982. The role of microarthropods and nematodes in decomposition in semi-arid ecosystems. Oecologia **55**, 303–310.
Hanlon, R. D. G., 1981a. Influence of grazing by Collembola on the activity of senescent fungal colonies grown on media of different nutrient concentration. Oikos **36**, 362–367.
– 1981b. Some factors influencing microbial growth on soil animal faeces I. Bacterial and fungal growth on particulate oak leaf litter. Pedobiologia **21**, 257–263.
– J. M. Anderson, 1979. The effects of Collembola grazing on microbial activity in decomposing leaf litter. Oecologia **38**, 93–100.
Huhta, V., & A. Koskenniemi, 1975. Numbers, biomass and community respiration of soil invertebrates in spruce forests at two latitudes in Finland. Ann. Zool. Fennici **12**, 164–182.
– H. Setälä, 1990. Laboratory design to simulate complexity of forest flow studiying the role of fauna in the soil processes. Biol. Fertil. Soils **10**, 155–162.
– R. Hyvönen, P. Kaasalainen, A. Koskenniemi, J. Muona, I. Mäkelä, M. Sulander & P. Vilkamaa, 1986. Soil fauna of Finnish coniferous forests. Ann. Zool. Fennici **23**, 345–360.
– H. Setälä & J. Haimi, 1988. Leaching of N and P from birch litter and raw humus with special emphasis on the influence of soil fauna. Soil Biol. Biochem. **20**, 875–878.
– D. H. Wright & D. C. Coleman, 1989. Characteristics of defaunated soil. I. A comparison of three techniques applied to two different forest soils. Pedobiologia **33**, 415–424.
Ineson, P., M. A. Leonard & J. M. Anderson, 1982. Effect of collembolan grazing upon nitrogen and cation leaching from decomposing leaf litter. Soil Biol. Biochem. **14**, 601–605.
Ingham, E. R., J. A. Trofymow, E. R. Ingham & D. C. Coleman, 1985. Interactions of bacteria, fungi and their nematode grazers: effects on nutrient cycling and plant growth. Ecol. Monogr. **55**, 119–140.
Klekowski, R. Z., L. Wasilewska & E. Paplinska, 1972. Oxygen consumption by soil-inhabiting nematodes. Nematologica **18**, 391–403.
Martikainen, E., & V. Huhta, 1990. Interactions between nematodes and predatory mites in raw humus soil – A microcosm experiment.
O'Connor, F. B., 1962. The extraction of Enchytraeidae from soil. *In:* P. W. Murphy, (ed.), Progress in soil zoology, London, pp. 279–285.
Persson, T., & U. Lohm, 1977. Energetical significance of the annelids and arthropods in a Swedish grassland soil. Ecol. Bull. (Stockholm) **23**, 3–211.
– E. Bååth, M. Clarholm, H. Lundkvist, B. E. Söderström & B. Sohlenius, 1980. Trophic structure, biomass dynamics and carbon metabolism of soil organisms in a Scots pine forest. Ecol. Bull (Stockholm) **32**, 419–459.
Petersen, H., 1975. Estimation of dry weight, fresh weight, and calorific content of various Collembolan species. Pedobiologia **15**, 222–243.
– & M. Luxton, 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos **39**, 287–388.
Ponge, J.-F., 1985. Etude écologique d'un humus forestier par l'observation d'un petit volume. II. La couche L_2 d'un moder sous *Pinus sylvestris*. Pedobiologia **28**, 73–114.
Santos, P. F., & W. G. Whitford, 1981. The effects of microarthropods on litter decomposition in a Chihuahuan desert ecosystem. Ecology **62**, 654–663.
Seastedt, T. R., 1984. The role of microarthropods in decomposition and mineralization processes. Ann. Rev. Entomol. **29**, 25–46.
Setälä, H., V. Huhta & J. Haimi, 1988. A microcosm study on the respiration and weight loss in birch litter and raw humus as influenced by soil fauna. Biol. Fertil. Soils **5**, 282–287.

– & V. HUHTA, 1990. Evaluation of the soil fauna impact on decomposition in a simulated coniferous forest soil. Biol. Fertil. Soils **10**, 163–169.
– E. MARTIKAINEN, M. TYYNISMAA & V. HUHTA, 1990. Effects of soil fauna on leaching of nitrogen and phosphorus from experimental systems simulating coniferous forest floor. Biol. Fertil. Soils **10**, 170–177.
SOHLENIUS, B., 1979. A carbon budget for nematodes, rotifers and tardigrades in a Swedish coniferous forest soil. Holarctic Ecology **2**, 30–40.
– 1985. Influence of climatic conditions on nematode coexistence: a laboratory experiment with a coniferous forest soil. Oikos **44**, 430–438.
STANDEN, V., 1978. The influence of soil fauna on decomposition by micro-organisms in blanket bog litter. J. Anim. Ecol. **47**, 25–38.
WOODS, L. E., C. V. COLE, E. T. ELLIOTT, R. V. ANDERSON & D. C. COLEMAN, 1982. Nitrogen transformations in soil as affected by bacterial-microfaunal interactions. Soil. Biol. Biochem. **14**, 93–98.

Synopsis: *Original scientific paper*

SETÄLÄ, H., M. TYYNISMAA, E. MARTIKAINEN & V. HUHTA, 1991. Mineralisation of C, N and P in relation to decomposer community structure in coniferous forest soil. Pedobiologia **35**, 285–296.

Two laboratory microcosm experiments were performed on raw humus forest soil, partially sterilized and re-inoculated with microbes (including protozoans), microbes with enchytraeids *(C. sphagnetorum)*, collembolans *(O. armatus)* or bacterial-feeding nematodes, each either alone or in combination, and bacterial feeders together with predatory nematodes. The presence of inoculated fauna increased the evolution of CO_2, and more so when two animal taxa were present in combination. The release of water-soluble N and P was lowest with bacterial-feeding nematodes alone. Other taxa either alone or together with the bacterial feeders increased the availability of nutrients when compared with bacterial feeders + microbes, but not when compared with microbes alone. Mutual relationships among the fauna were considered to be of importance in the decomposition processes.

Key words: Mineralisation, Decomposition, Soil fauna, Community Structure, Raw humus, Forest soil, Microcosm.

Address: H. SETÄLÄ (corresponding author), M. TYYNISMAA, E. MARTIKAINEN, V. HUHTA, Department of Biology, University of Jyväskylä, Jyväskylä, SF-40100, Finland.